

ENOPLOMETOPUS A. MILNE-EDWARDS, 1862 (CRUSTACEA: DECAPODA: NEPHROPOIDEA) FROM THE PHILIPPINES, WITH DESCRIPTION OF ONE NEW SPECIES AND A REVISED KEY TO THE GENUS

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ABSTRACT

Two species of reef lobsters of the genus *Enoplometopus* have been found in tangle net catches in Panglao, central Philippines. One, the supposedly rare species *Enoplometopus crosnieri* Chan and Yu, 1988, is actually rather common there. The other species is new to science and is morphologically close to the Atlantic *Enoplometopus callistus* Intès and Le Loeuff, 1970, but differs in the shape of the large chelipeds and body coloration. The only species previously described from the Philippines is *Enoplometopus chacei* Kensley and Child, 1986, and its holotype is re-examined. The intermediate characters exhibited in *E. crosnieri*, *E. callistus*, and the present new species show that the two subgenera proposed for *Enoplometopus* cannot be recognized. A revised key to the genus is provided.

The decapod crustacean fauna of Balicasag Island in the Bohol Sea of the Philippines has been the subject of numerous studies over the last decade as a result of the activities of various Philippine, Japanese, Singapore, and French carcinologists. These studies have resulted in numerous papers and the discovery of dozens of new records, genera and species (Takeda and Manuel, 2000; Ng and Liao, 2002; Galil, 2003; Ng, 2003; Ng and Ho, 2003; Ah Yong, 2004; Crosnier and Ng, 2004; Galil and Takeda, 2004; McLay and Ng, 2004, 2005; Komatsu et al., 2005; Ng and McLay, 2005; Galil and Ng, 2007; Manuel-Santos and Ng, 2007; Richer de Forges and Ng, 2007a–c). The fishermen on this island use long tangle nets set against the steep slopes of the reef-dropoff, sometimes to depths exceeding 400 m, targeting commercially valuable molluscs for the lucrative shell-trade (see McLay and Ng, 2004, 2005; Ng et al., in press).

One of the more common macruran decapods at Balicasag is the recently described and supposed rare reef lobster *Enoplometopus crosnieri* Chan and Yu, 1998, originally described from one specimen from Taiwan (Chan and Yu, 1998) and later also found in Australia and French Polynesia (Poupin, 2003). A second species of *Enoplometopus* was also present, but was comparatively much rarer. It was initially identified to *Enoplometopus occidentalis* (Randall, 1840), a common and widespread species from the Indo-West Pacific, but it became clear after a detailed study, that it actually represents a new species close to *Enoplometopus callistus* Intès and Le Loeuff, 1970. This latter species was described from the Atlantic and had been placed in a different subgenus or even genus (i.e., *Hoplometopus* Holthuis, 1983) from *E. occidentalis* by some authors (e.g., Holthuis, 1983; de Saint Laurent, 1988). As pointed out by Poupin (2003), *E. callistus*, like *E. crosnieri*, has intermediate characters between the two subgenera established by Holthuis (1983). The present discovery of one more species with “intermediate” generic characters further negates the necessity of splitting *Enoplometopus* s.l.

The present work describes the new *Enoplometopus* and formally reports *E. crosnieri* from Balicasag Island. The holotype of *Enoplometopus chacei* Kensley and Child,

1986, the only species previously described from the Philippines, is also re-examined. The characters used to separate the species of *Enoplometopus* are reassessed and a revised key is provided for the 12 known species.

MATERIAL AND METHODS

Specimens examined are deposited in the Crustacean Collection of the National Museum, Manila (NMCR); National Taiwan Ocean University, Keelung (NTOU); Raffles Museum of Biodiversity Research, National University of Singapore (ZRC); and Muséum National d'Histoire Naturelle, Paris (MNHN). The carapace length (cl) was measured dorsally from the posterior point of the orbital margin to the posterior margin of the carapace. The term "setal pit" refers to areas where long stiff setae grow out, which is generally between two closely adjacent tubercles.

The following species deposited at the NTOU, ZRC and MNHN were used for comparisons and key construction: *Enoplometopus antillensis* Lütken, 1865 (Guadeloupe: 1 male cl 30.6 mm, MNHN; Ascension Island: 1 male cl 26.9 mm, MNHN; Gulf of Guinea: 1 female cl 20.2 mm, MNHN), *E. callistus* (Gulf of Guinea: 2 males cl 42.0 mm (holotype) and 44.7 mm, 1 female cl 53.8 mm, MNHN), *Enoplometopus daumi* Holthuis, 1983 (Philippines: 1 ovigerous female cl 18.5 mm, NTOU; aquarium shops in Taiwan and Singapore, provenance unknown: 3 males cl 13.6–18.6 mm, 4 females (1 molt only) cl 13.1–15.7 mm, NTOU), *Enoplometopus debelius* Holthuis, 1983 (Aquarium shops in Singapore, provenance unknown: 2 males cl 11.2–13.8 mm, 1 female cl 12.3 mm, NTOU), *Enoplometopus gracilipes* (de Saint Laurent, 1988) (French Polynesia: 1 male cl 46.1 mm, NTOU), *Enoplometopus holthuisi* Gordon, 1968 (Austral Islands: 1 male cl 28.6 mm, MNHN), *E. occidentalis* (Taiwan: 4 males cl 41.6–46.5 mm, 4 females cl 31.9–44.8 mm, NTOU, 2 males cl 39.5–40.6 mm, ZRC; Hawaii: 2 males cl 37.3–41.4 mm, ZRC; aquarium shops in Taiwan and Singapore, provenance unknown: 1 male cl 28.5 mm, 1 female cl 14.3 mm, NTOU), *Enoplometopus pictus* A. Milne-Edwards, 1862 (La Réunion: 1 male holotype cl 39.9 mm, MNHN).

SYSTEMATICS

Enoplometopus macrodontus new species

(Figs. 1–3)

Material Examined.—Holotype: Male (cl 39.3 mm), Balicasag Island, near Panglao, Bohol, Visayas, central Philippines, from tangle nets, coll. local fishermen, June 2002 (NMCR).

Paratypes: Same locality as holotype, June 2002, 1 male (cl 35.9 mm) (MNHN, ex-ZRC 2008.0446); 28 November 2001, 1 male (cl 58.1 mm) (NTOU M00700, ex-ZRC 2001.0954), 1 ovigerous female (cl 39.5 mm) (MNHN, ex-ZRC 2001.0954); 1–5 March 2004, 2 males (cl 36.6–45.7 mm), 2 females (cl 27.8–41.4 mm) (ZRC 2008.0447). Momo Beach, northern Panglao, Bohol, Visayas, central Philippines, ca. 160 m, tangle nets, coll. J. Arbusto, 9 January 2007, 1 ovigerous female (cl 46.7 mm) (NTOU M00701, ex ZRC 2008.0448).

Type Locality.—Balicasag Island and Panglao, Bohol, Visayas, central Philippines, probably from depths of 90–200 m.

Etymology.—The Latin *macrodontus* (large teeth) refers to the teeth on the dorsal hinge of the fingers of the large chelae becoming very large and projecting upwards in large males of this species. Such a character is unique in *Enoplometopus*.

Size.—Moderately large for the genus, with largest male cl 58.1 mm and largest females cl 46.7 mm.

Distribution.—So far only found from Balicasag Island, and the rocky areas of the nearby Momo Beach on the main island of Panglao, Philippines.

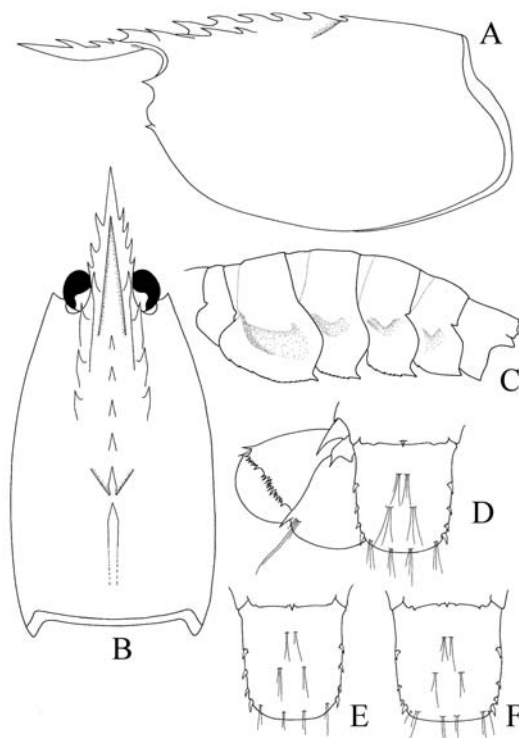


Figure 1. *Enoplometopus macrodontus* new species. Balicasag Island, Philippines, setae mostly omitted: A–D. holotype male cl 39.3 mm (NMCR); E. paratype male cl 36.6 mm (ZRC); F. paratype male cl 58.1 mm (NTOU M00700). (A) carapace, lateral; (B) carapace, dorsal; (C) abdomen, lateral; (D) posterior abdominal tergite VI, telson and left uropods, dorsal; (E–F) posterior abdominal tergite VI and telson, dorsal.

Description.—Size moderately large. Body pubescent, with numerous long stiff setae. Rostrum elongated, distinctly overreaching antennular peduncle, armed with 3 or 4 pairs (rarely 2 or 5 on one side) of lateral teeth. Carapace (Fig. 1A,B) with large supra-ocular spine and 1 large intermediate, 5 median, 2 lateral and 1 postcervical teeth; all teeth well-developed; intermediate tooth more or less as large as supra-ocular spine, extending to nearly anterior margin of eye, ridge continues behind intermediate tooth generally smooth; median teeth similar in size, only anteriormost tooth sometimes slightly smaller, without trace of tubercle anterior to it, posteriormost tooth with posterior end on cervical groove; postcervical tooth smaller than median teeth but very well-defined. Antennal spine large, strongly bent inwards. Small but distinct branchiostegal spine generally present. Dorsal surfaces of rostrum and carapace with scattered long stiff setae. Eye well-developed, subspherical. Scaphocerite, including distolateral tooth, more or less reaching tip of antennular peduncle. Antennal peduncle slightly over-reaching scaphocerite, basicerite spine well developed, acute.

Abdomen with some long stiff setae (more numerous posteriorly), bearing a low blunt median keel on somites II to VI, depressions generally shallow except anterior depression on pleuron II slightly deeper; pleura II to VI terminate as distinct spines that become progressively smaller posteriorly; anterior margin of pleura II to V finely denticulate, posterior margin smooth, not notched (Fig. 1C). Posterior margin of tergite VI with only basal tubercles (rather sharp in large individuals) at submedian and lateral setal pits, without spines. Telson rectangular, slightly longer than wide; bearing 2 pairs of movable lateral spines and 2 pairs of movable posterolateral spines (Fig. 1D,E,F); 2 posterolateral spines always next to each other, with inner one longer; 2 lateral spines always far apart, one situated at basal 1/3–2/5 and

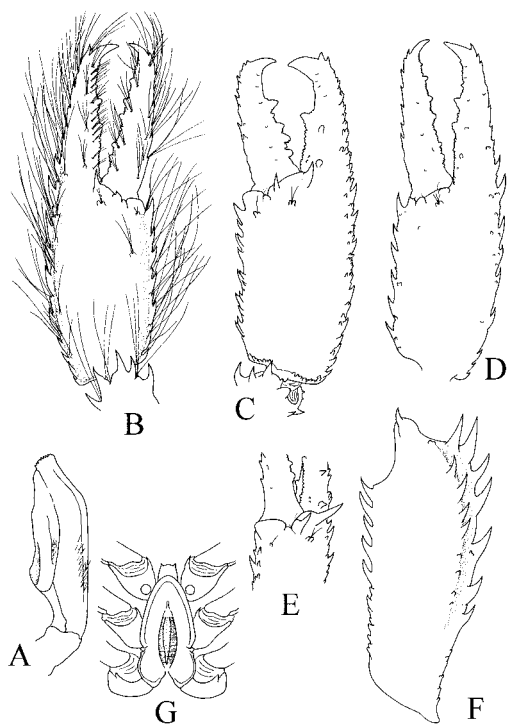


Figure 2. *Enoplometopus macrodontus* new species. Balicasag Island, Philippines: A, C, E. paratype male cl 58.1 mm (NTOU M00700); B, D, F. holotype male cl 39.3 mm (NMCR); G. paratype ovigerous female cl 39.5 mm (MNHN). (A) right pleopod I, outer; (B) left large chela, dorsal; (C) right large chela, dorsal, setae mostly omitted; (D) left large chela, ventral, setae mostly omitted; (E) hinge of fingers of right large chela, dorso-inner view, setae mostly omitted; (F) merus of left large chela, outer, setae mostly omitted; (G) receptaculum seminis, ventral.

another at basal 3/5–3/4 of lateral margin, latter one sometimes quite close to posterolateral spines. Uropods with protopodite divided into 2 lobes, each with an elongate spine-like apex, otherwise with margins smooth, outer spine at least twice as long as ventral spine of pleuron II; endopod shorter than telson and bearing a posterolateral spine; exopod slightly longer than telson, with distinct diaeresis and strong outer spine that is accompanied with a movable spine. Pleopod I (Fig. 2A) developed into ridged plate in males, distally not indented, resembling broad triangle, posterodistal margin concave, about 2.5 times wider than anterodistal margin, anterodistal margin minutely denticulated. Eggs small, numerous, about 0.55 mm in diameter (freshly preserved).

Maxilliped III over-reaching scaphocerite more or less by distal segment; carpus with distinct distoventral spine; merus bearing 2 distoventral spines (distal spine very large) and 1 disto-outer spine (rarely absent); ischium with 1 disto-outer and 1 distoventral spines, inner margin serrated with minute denticles; basis bearing distoventral spine. First chelipeds exceeding scaphocerite by about carpus and chela, left and right generally similar in size and shape; chelae (Fig. 2B,C,D) either both cutting or both crushing (in largest male); rarely with 1 cutting and 1 crushing (only in second largest male). Cutting chela 3.5–4.8 times longer than width, fingers as long as or slightly longer than palm; tips of fingers elongate, curving inwards; fixed finger slightly longer than movable finger; outer margins of fingers densely covered with long stiff setae, appears somewhat serrated with numerous setal pits, that of fixed finger often with 1 or 2 well-defined teeth both distally and basally, that of movable finger with 0–2 well-defined teeth distally; dorsal and ventral surfaces of fingers not ridged; cutting edges densely serrated with small teeth, with some larger teeth inserted at regular intervals, also bearing



Figure 3. *Enoplometopus macrodontus* new species. Color in life. Momo Beach, northern Panglao, Philippines, ovigerous female paratype cl 46.7 mm (NTOU M00701). (A) dorsolateral view; (B) posterolateral view.

some long stiff setae; dorsal and ventral surfaces of palm smooth but pubescent; dorsal hinge of fingers armed with 2 large teeth, outer one shorter, sometimes blunt, often directed upwards, inner one elongate, sometimes very long; ventral hinge with 0 or 1 (mostly 0) spine and 1–5 (rarely 0) tubercles near inner base of fixed finger; area slightly behind both dorsal and ventral hinges of fingers having a prominent setal pit. Crushing chela different from cutting chela, being broader, 3.2–3.6 times longer width, fingers of similar length and shorter than palm; cutting edges with teeth broader but blunt, distal 1/3 margin devoid of teeth and regularly concave; 2 teeth on dorsal hinge of fingers very large, both directed upwards (Fig. 2E). Carpus and merus of first cheliped almost completely covered with large and small teeth along all margins except posterior 1/2–1/3 of dorsal margin of merus which is finely denticulate or smooth (Fig. 2F); ischium with entire inner margin serrated, outer margin only bearing a large distal tooth. Pereiopods II to V subchelate, with distal prolongations of propodi becoming less developed posteriorly, except that of pereopod V in females being short, spoon-shaped.

Receptaculum seminis (Fig. 2G) on thoracic sternum with blunt anterior end, posterior end wider, triangularly notched, lateral margins convex but deeply notched at posterior 1/3, with 1 small spine on posterior part.

Coloration in Life (Fig. 3).—Body generally reddish-orange with few white spots and lines. Carapace mostly uniformly orange, with one moderately large white spot behind branchiostegal spine, small white spots also distributed along anterolateral margin behind orbit and branchiostegal spine, dorsal ridges and posterior margin alternated with red and white. Rostrum with 3 white transverse bands: at base of supraocular spines (thickest), around mid-rostrum, and subdistally; teeth reddish, sometimes with white tips, tip of postcervical tooth always white. Antennular and antennal flagellae not banded; antennular flagella reddish at basal 3/4 but inner margin whitish, distal 1/4 entirely whitish; antennal flagella with distal half whitish, basal half with outer part reddish and inner part whitish. Eyes dark brown. Abdomen with tergum orange except median keel alternated with red and white; pleura reddish and with large white spots at the junctions between tergites and pleura, except for somite II which has a large white spot at anterior pleuron; ventral spines of pleura also whitish. Tailfan reddish, covered with an irregular white transverse band at distal 1/3. Maxilliped III reddish, anterior margins of propodus and merus whitish, dorso-outer spine on ischium also whitish. Large cheliped reddish except for palm and carpus mostly orange, fingers with white tips and white bands medially, teeth on margins red (more often) or white, some short transverse white lines also extended from margins of palm and merus, distal part of ischium with a large white spot, teeth on dorsal hinge of fingers always reddish. Pereiopods II to V reddish and each covered with 3 thin white bands on merus and ischium, bases of propodi also somewhat whitish. Long stiff setae golden brown. Eggs reddish-brown.

Remarks.—In the largest female specimen from Balicasag (cl 41.4 mm, ZRC 2008.0447), the rostrum only has 1 or 2 lateral teeth (vs generally 3 or 4 lateral teeth) and the left maxilliped III has fewer spines (i.e., merus with only one distoventral spine and ischium lacking a distoventral spine vs ischium normally bearing a distoventral spine). On the other hand, the male of cl 36.6 mm (ZRC 2008.0447) has two intermediate teeth on the left side (vs normally 1 intermediate tooth). The variations observed in these specimens are likely to be abnormal or perhaps due to regeneration after damage. In the largest male (cl 58.1 mm, NTOU M00701), there are two large and dorsally directed spines on the dorsal surface of the right fixed finger (Fig. 2C,F) and the ridge behind the intermediate tooth is slightly jagged. Furthermore, in this largest male, the inner lobe of the protopodite of the uropod has the margins tuberculate instead of smooth, and there is a sharp dorsal tubercle present on the outer lobe. The differences exhibited in the largest male are, however, likely to be associated with its size.

The present new species can be readily separated from the other species of the genus in the Indo-West Pacific by having one postcervical tooth on the carapace and two lateral spines at the telson. Surprisingly, an examination of the two Atlantic species *E. antillensis* and *E. callistus* (Figs. 4A–F, 5A) showed that the new species is very close to the latter, and these two species are unique in the genus in having the anterior margins of the abdominal pleura finely denticulate (particularly at the second pleuron) instead of smooth, even in adults. The most obvious differences found between the new species and *E. callistus* (Gulf of Guinea: 2 males cl 42.0 mm (holotype) and 44.7 mm, 1 female cl 53.8 mm, MNHN As57, As 627) are on the large cheliped. The dorsal margin of the merus of the large cheliped is armed with spines almost over the entire length (always more than distal 3/4 length) in *E. callistus* (Fig. 4E) but only along the distal 1/2–2/3 in the new species (Fig. 2F). In *E. callistus*, the large chela has a small inner spine and an outer blunt protuberance at both the dorsal and ventral hinges (Figs. 4D, 5A). In the new species, the dorsal hinge generally has two spines (Fig. 2B) that become remarkably large and directed upwards in large individuals (Fig. 2C). The other differences found between the new species and *E. callistus* are that in *E. callistus*, the ventral surface of the fixed finger of the large chela has no tubercle (Fig. 5A), the ridge behind the intermediate tooth and the posterior margins of abdominal pleura are somewhat denticulate (Fig. 4B,C), and the spine-like apices of the protopodite of the uropod (Fig. 4F) are relatively shorter and

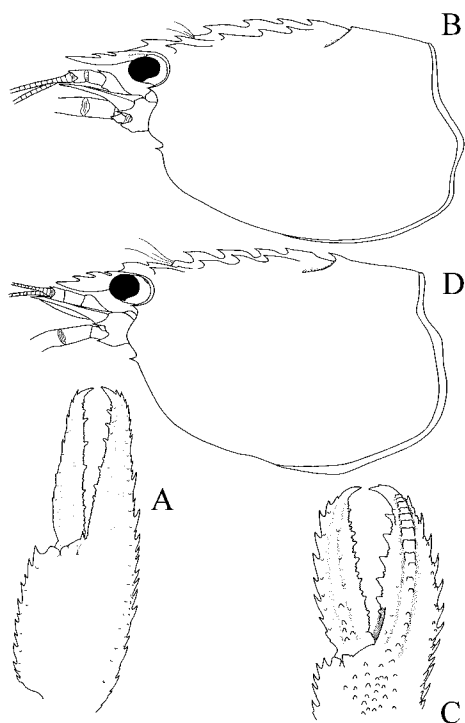


Figure 4. *Enoplometopus callistus*, Gulf of Guinea, male, cl 44.7 mm (MNHN As 627), setae mostly omitted. (A) carapace, lateral; (B) carapace, dorsal; (C) abdomen, lateral; (D) left large chela, dorsal; (E) merus of left large chela, outer; (F) posterior abdominal tergite VI, telson and left uropods, dorsal.

as long as the ventral spine of the pleuron II in two (both males) of the three specimens examined. Although the outer margin of the movable finger in *E. callistus* is entirely spinose in the holotype, the other two specimens examined only have distinct spines at the subdistal part of the outer margin of movable finger (Figs. 4D, 5A, see also Poupin, 2003: fig. 8A,D) and are not very different from the new species (Fig. 2B,C,D). The coloration of *E. callistus* is very different from the new species in the whole body, including the large chelipeds, being uniformly with red blotches, the dorsal surfaces of the fingers of large chela having four distinct white spots (excluding the white tips), the antennular flagella and pereopods II to V being entirely banded with red and white, and the tailfan having white spots on the margins but lacking a transverse white band (cf. González Pérez, 1995: photographs 74–75; Debelius, 1999: 44).

Although this new species was initially mistaken as *E. occidentalis* because it lacked a large ocellus on the carapace when preserved, a fresh specimen later obtained (Fig. 3) showed that its body coloration is actually very different from *E. occidentalis*. For example, in *E. occidentalis* (cf. Chan and Yu, 1993: 102; Allen and Steene, 1994: 145; Debelius, 1999: 205) the body is densely covered with red dots, there is no white band on the large chelae, the white spot on the lateral carapace is situated far behind and at about mid-carapace, pereopods II to V entirely banded with orange and white, and the abdomen has many more white spots (e.g., a pair of longitudinal rows of white spots adjacent to the median keel and along the margins of pleura).

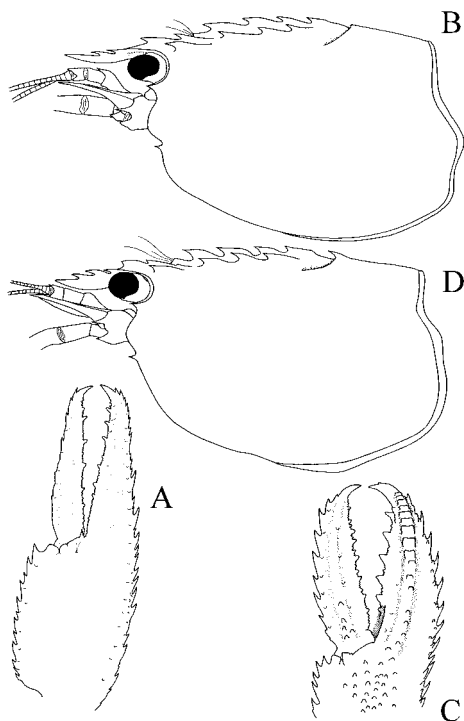


Figure 5. (A) *Enoplometopus callistus*, Gulf of Guinea, male cl 44.7 mm (MNHN As 627), left large chela, ventral, setae mostly omitted; (B) *Enoplometopus chacei*, Batan Island, Philippines, holotype male cl 36.7 mm (NMCR), carapace, lateral, setae mostly omitted; (C) *Enoplometopus crosnieri*, Taiwan, male cl 62.8 mm (NTOU M00602), fingers of left chela, ventral, setae mostly omitted; (D) *Enoplometopus occidentalis*, Taiwan, female cl 42.9 mm (NTOU M00152), carapace, lateral, setae mostly omitted.

Enoplometopus chacei Kensley and Child, 1986

(Fig. 5B)

Enoplometopus chacei Kensley and Child, 1986: 520, figs. 1–2 (type locality: Philippines).

Material Examined.—Holotype: Male (cl 36.7 mm), Batan Island, Philippines, by hand net in 2 m, 8 June 1985 (NMCR).

Distribution.—Only known with certainty from the Philippines.

Remarks.—A re-examination of the holotype showed that the original description and figures provided by Kensley and Child (1986) are generally accurate, except the anterior tubercle in front of the median teeth on the carapace is small but distinct. Furthermore, the postcervical “tubercle” is actually rather large (as large as the last median tooth) but flattened (Fig. 5B). There are still some color patterns on the holotype and it resembles the original figure provided by Kensley and Child (1986: fig. 1). The color spots on the lower lateral carapace are still visible as orange dots and mainly distributed at the anteroventral part of the carapace. This confirms that *E. chacei* is different from *E. pictus* in coloration as well, and is most similar to *E. daumi*

and *E. debelius* instead. Apart from having a very different coloration in life, *E. chacei* differs from *E. daumi* and *E. debelius* in having the rostrum relatively longer (exceeding vs not exceeding antennular peduncle) and bearing fewer lateral teeth (2 pairs vs generally 3 pairs). It also appears to reach a larger adult size (cl 36.7 mm vs < cl 26 mm for *E. daumi* and *E. debelius*, cf. Holthuis, 1983).

Enoplometopus crosnieri Chan and Yu, 1998

(Fig. 5C)

Enoplometopus crosnieri Chan and Yu, 1998: 184, figs. 1–3 (type locality: Taiwan); Poupin, 2003: 645, figs. 2–3.

Enoplometopus sp. nov.—Poupin et al., 1990: pl. III-c; Poupin, 1996: pl. V-h.

Material Examined.—Philippines: Balicasag Island, near Panglao, Bohol, Visayas, from tangle nets, coll. local fishermen, December 2000, 1 male (cl 43.8 mm), 1 ovigerous female (cl 37.1 mm), 1 female (cl 28.9 mm) (NTOU, ex-ZRC 2001.0322); 28 November 2001, 5 males, 2 females (ZRC 2001.0954); July 2003, 2 males, 1 female (ZRC 2003.0750); 1–5 March 2004, 1 ovigerous female (ZRC 2004.0683); 28 May 2004, 1 male, 2 females (ZRC 2008.0534). Taiwan: fish market at Hepingdao, Keelung, probably from lobster trap net at about 100 m deep, January 1997, holotype ovigerous female (cl 55.4 mm, with a molt cl 54.7 mm) (NTOU M00595, ex-NTOU 1887-1-H); May 2000, 1 male (cl 62.8 mm) (NTOU M00602).—Taipei Sea Life, probably originated from Hualien, February 1999, 1 female (cl 52.2 mm) (NTOU M00604). French Polynesia: Frv “Marara”, stn 193, 9 September 1989, 1 male (cl 39.0 mm) (MNHN As560); stn 288, 28 August 1990, 2 males (cl 45.6–47.9 mm), 3 ovigerous females (cl 35.1–43.6 mm) (MNHN As570), 1 male (cl 40.1 mm), 2 ovigerous females (cl 41.1–46.1 mm) (MNHN As571).—MUSORSTOM 9, stn CP1227, 30 August 1997, female large chelae only (MNHN As616).

Distribution.—West and central Pacific. Known with certainty from Taiwan, the Philippines, Australia (Timor Sea) and French Polynesia, at depths of 84–120 m.

Remarks.—The present specimens from the Philippines agree well with the original description by Chan and Yu (1998) and the additional observations by Poupin (2003). However, with the many males now found, it is observed that there is marked sexual dimorphism at the ventral surface of the fixed finger of the large chela in this species. This surface is smooth in females but covered with a longitudinal row of stair-like strong ridges along the distal half of the fixed finger in males (Fig. 5C). Such sexual dimorphism and stair-like ridges are not known in any other species of *Enoplometopus*. As these ridges are only developed in males, they may serve some stridulatory functions, either related to mate or space competition. Observations on live male specimens of *E. crosnieri* will be necessary to help throw light on this.

Poupin (2003) mentioned that the dorsal surface of the palm of the large chela is nearly smooth in specimens smaller than cl 40 mm. However, all the specimens examined here (including those of Poupin, 2003) have this surface sharply tuberculate even in the smallest female of cl 28.9 mm (though the tubercles are sometimes smaller in smaller specimens). Only the margins of the basal lobe of the endopod of the uropod become less spiny in smaller individuals.

Some *Enoplometopus* postlarvae or very early juveniles were sent to the first author by J. Poupin. Three of them (French Polynesia, stn CS418+CS539, 2 specimens, cl 12.8–13.7 mm; stn CS425 (4FT), 1 specimen, cl 9.4 mm) have the same arrangement of spines and teeth on the rostrum, carapace and telson (lateral spines indistinct for the smallest specimen) as in *E. crosnieri*. Nevertheless, their rostrum is relatively longer and bear small ventral teeth, the cervical groove is rather indistinct, the ischium of maxilliped III lacks distoventral spine, the abdominal pleura are sharply pointed ventrally and with the anterior margins denticulate (the smallest specimen also has a very strong median keel on the abdomen). The most striking difference, however, is the posterior margin of the abdominal tergite VI bearing a pair of large submedian spines in these postlarvae. If these specimens are really the postlarvae of *E. crosnieri*, their characters will be significant in understanding the relationships of the species in the genus, particularly as *E. crosnieri* is intermediate between the two subgenera, *Enoplometopus* (*Enoplometopus*) A. Milne-Edwards, 1862, and *Enoplometopus* (*Hoplometopus*) Holthuis, 1983 (see Chan and Yu, 1998; Poupin, 2003).

DISCUSSION

As discussed by Poupin (2003), of the four characters (number of intermediate teeth, postcervical teeth, lateral telson spines and shape of abdominal pleura) which have been used by Holthuis (1983) to separate the two subgenera, *Enoplometopus* s.s. and *Hoplometopus*, only two are still valid. This is because of the intermediate characters exhibited by *E. crosnieri*, *E. callistus* (see Poupin, 2003), and now, *E. macrodontus*, new species. After examining more specimens and species, we note that the shape of the abdominal pleura in *E. crosnieri* is also somewhat intermediate between the two subgenera. The abdominal pleural spines are very long in *E. antillensis*, *E. holthuisi*, and *Enoplometopus voightmanni* Türkay, 1989, with the posterior margins of pleura deeply notched. The abdominal pleura have the ventral spines moderately long and the posterior margins slightly notched in *E. gracilipes*. The abdominal pleural spines in *E. callistus* and *E. macrodontus* are not long and the posterior margins of the pleura are not notched. The ventral margins of the abdominal pleura in the species of *Enoplometopus* s.s. are either bluntly pointed or terminating as minute spines. The abdominal pleura of *E. crosnieri* terminate as small spines slightly larger than those of species of *Enoplometopus* s.s. but are slightly smaller than those of *E. macrodontus* and *E. callistus*. For the number of spines on the lateral margin of telson, sometimes the distal lateral spine is quite close to the posterolateral spines in *E. macrodontus* and *E. callistus* (Figs. 1F, 4F), hence making the use of this character as a taxonomic tool rather difficult. As few specimens of *Hoplometopus* species have been examined, it is not known if the variations in the position of the lateral telson spines exhibited in *E. macrodontus* and *E. callistus* also occur in other species.

Poupin (2003) proposed that the shape of the large chelae is an important character for separating the species of *Enoplometopus*. He noted that the surface structure of the large chela (i.e., tuberculate or smooth) is generally constant for most species except in juveniles of certain species such as *E. occidentalis*, *E. debelius*, and *E. dau-mi*. On the other hand, the above-mentioned postlarvae of probably *E. crosnieri* have the large chela almost entirely covered with distinct and sharp tubercles. The relative breadth of the large chela, however, shows substantial variation when more specimens were examined. In *E. macrodontus*, it can be 3.2–4.8 times as long as broad.

The Austral Island specimen of *H. holthuisi* in Poupin (2003) also has a much shorter large chela than the holotype (see Poupin, 2003: fig. 7C,G). The specimens of *E. antillensis* and *E. callistus* examined have the large chela 3.7–4.4 and 2.6–4.5 times as long as wide, respectively, instead of 3.6–4.0 and 2.6–3.9 times as long as wide as mentioned by Poupin (2003). The use of the strength of the teeth on the outer margin of the movable finger can also be confusing as the separation between basal tubercles of setal pits and teeth is sometimes quite vague. For example, the outer margin of the moveable finger in *E. callistus* is heavily spinose in the holotype male (Poupin, 2003: fig. 8A) but only has a few distinct spines in the other two specimens examined (Figs. 4D, 5A, Poupin, 2003: fig. 8D). Nevertheless, it appears that the spination on the outer margin of the movable finger is still useful in the separation of some other species. The shape of the pleopod I in males and the thelycum of females appear to be useful for separating the groups in the genus. However, the shapes of the male pleopod I and female thelycum are not known for all the species, so the use of these characters is less convenient when they are used in keys.

Enoplometopus crosnieri is an unusual species in the genus. Apart from having a combination of characters intermediate between the subgenera *Enoplometopus* s.s. and *Hoplometopus*, it is unique in having marked sexual dimorphism and bearing probable stridulating organs on the large male chelae. Although Chan and Yu (1998) and Poupin (2003) placed *E. crosnieri* closer to the subgenus *Enoplometopus* s.s., the ischium of the maxilliped III of *E. crosnieri* has a distoventral spine. The possession of a distoventral spine on the ischium of the maxilliped III is supposedly a character associated with *Hoplometopus*, and is otherwise absent in all other species of *Enoplometopus* s.s. This clearly poses some problems with this subgeneric classification. Detailed studies on the phylogenetic relationships of the species of *Enoplometopus* s.l. will be necessary to determine if the genus should be separated into two or more groups and what characters should then be used for such separations. Nonetheless, the two groups, *E. chacei*/*E. daumi*/*E. debelius* and *E. antillensis*/*E. holthuisi*/*E. voightmanni*, appear to exhibit the two extremes of morphological variations in these lobsters.

All *Enoplometopus* species known have very distinctive and diagnostic colorations. Live or fresh specimen and even preserved specimens with color pattern remained can be easily separated by coloration (Table 1). However, several species are morphologically extremely similar, such as *E. chacei*/*E. daumi*/*E. debelius*, *E. holthuisi*/*E. voightmanni* and the present new species, *E. macrodontus*, with *E. callistus*. Table 2 shows the distinguishing characters amongst the 12 species of *Enoplometopus* and a revised key to the genus is given below. Attention should be paid to the spines on the large chela and the posterior margin of the abdominal tergite VI. As mentioned above, basal tubercles of setal pits can sometimes be very large and sharp resembling spines, but they are always low. Here a “spine” is defined as either an elongate structure or with tip far from the margin where the spine developed.

Table 1. Distinguishing coloration and geographical distribution of species of *Enoplometopus*.

	Lateral carapace	Abdomen	Antennular flagellae	Large chelae (PD) fingers	Walking legs (PII-V)	Distribution
<i>E. crosnieri</i>	with large ocellated spot	many white spots on tergites and pleura	not banded	distinctly banded	banded only at basal segments	Western Pacific
<i>E. macrodontus</i>	only one moderate large white spot	many white spots on tergites and pleura	not banded	only with 1 white band	banded only at basal segments	Philippines only
<i>E. callistus</i>	covered with many red spots	white spots only on pleura	banded	distinctly banded	entirely banded	East Atlantic
<i>E. occidentalis</i>	only one moderate large white spot	many white spots on tergites and pleura	not banded	indistinctly banded	entirely banded	Indo-West Pacific
<i>E. pictus</i>	covered with many blue-margined white spots	many blue-margined white spots on tergites and pleura	not banded	more or less purplish-red	not banded	Réunion only
<i>E. chacei</i>	only some orange-red spots at anteroventral region	white spots only on pleura	not banded	indistinctly banded	not banded	Philippines only
<i>E. debelius</i>	uniformly covered with purple spots	uniformly covered with purple spots	not banded	banded	not banded	West Pacific
<i>E. daumi</i>	covered with vertical streaks	many white spots on tergites and pleura	not banded	banded	not banded	Indo-West Pacific
<i>E. gracilipes</i>	uniformly covered with red spots	uniformly covered with red spots	not banded	distinctly banded	entirely banded	French Polynesia, New Caledonia and Japan Atlantic
<i>E. antillensis</i>	with large circular marking	many white spots on tergites and pleura	not banded	distinctly banded	entirely banded	Indo-West Pacific
<i>E. holthuisi</i>	with large ocellated spot	many white spots on tergites and pleura	banded	distinctly banded	entirely banded	Indo-West Pacific
<i>E. voigtmanni</i>	with network of streaks	many white spots on tergites and pleura	not banded	distinctly banded	entirely banded	Indo-West Pacific

KEY TO SPECIES OF *ENOPLOMETOPUS*

- 1a. Carapace at most with 1 postcervical tooth, abdominal pleura terminating into blunt angle or short spines, with posterior margin not notched 2
- 1b. Carapace with 2 postcervical teeth, abdominal pleura terminating in elongate spine, with posterior margin notched 9
- 2a. Carapace with 1 intermediate tooth and 2 lateral teeth, ischium of maxilliped III bearing a distoventral spine 3
- 2b. Carapace with 2 intermediate teeth and 3 lateral teeth, ischium of maxilliped III without distoventral spine 5
- 3a. Carapace with 6 median teeth, surfaces of large chela sharply tuberculate, telson with 1 lateral spine; lateral carapace with very large ocellus *E. crosnieri*
- 3b. Carapace with 5 median teeth, surfaces of large chela smooth, telson with 2 lateral spines; lateral carapace without large ocellus 4
- 4a. Merus of large cheliped with dorsal margin only bearing spines at anterior 1/2–2/3, dorsal hinge of fingers generally bearing 2 spines that are massive in large males; most parts of carapace, abdominal tergum and dorsal surface of palm of large cheliped evenly orange without any red spots, antennular flagella and distal segments of pereopod II to V not banded *E. macrodontus*
- 4b. Merus of large cheliped with dorsal margin almost entirely (i.e., more than 3/4 length) spinose, dorsal hinge of fingers always with 1 small spine; body uniformly covered with red spots, entire antennular flagella and pereopods II to V banded *E. callistus*
- 5a. Postcervical tooth well-developed with tip high (carapace with 5 median teeth, anterior-most tooth sometimes as an elevated triangular plate, Fig. 5D); body orangish-red, with some conspicuous white spots on abdomen, fewer on carapace, pereopods II to V banded *E. occidentalis*
- 5b. Postcervical tooth indistinct or very low and more or less level with carapace; pereopods II to V not banded 6
- 6a. Carapace with 5 median teeth (anterior tooth well developed) outer margin of movable finger heavily spinose over entire length; body purplish-red with blue-margined white spots, posterior margin of tailfan bluish *E. pictus*
- 6b. Carapace with 4 median teeth, sometimes with 1 rudimentary anterior tubercle, outer margin of movable finger only bearing distinct spines distally, rarely also basally; posterior margin of tailfan not bluish 7
- 7a. Rostrum bearing 2 lateral teeth, overreaching antennular peduncle, large species, cl reaching 36.7 mm; body orangish-red and with color spots limited to lower carapace and abdomen *E. chacei*
- 7b. Rostrum generally bearing 3 lateral teeth, not exceeding antennular peduncle, small species, cl < 26 mm 8
- 8a. Rostrum broadly triangular, 1.4–1.6 times as long as basal width, tip of postcervical tooth distinctly separated from carapace; body whitish, uniformly covered with purple spots *E. debelius*
- 8b. Rostrum more elongate, 1.7–2.0 times as long as basal width, tip of postcervical tooth generally almost level with carapace; body purplish with carapace bearing vertical reddish brown streaks, abdomen distributed with many white spots *E. daumi*
- 9a. Posterior margin of abdominal tergite VI without distinct spine, abdominal pleura with posterior margin slightly notched; body uniformly covered with red spots *E. gracilipes*
- 9b. Posterior margin of abdominal tergite VI bearing 2 distinct spines, abdominal pleura with posterior margin deeply notched; body not uniformly covered with red spots 10
- 10a. Outer margin of fixed finger of large chela distributed with distinct spines over entire length; both antennular flagella and palm of large chela not banded, lateral carapace with large circular marking *E. antillensis*

- 10b. Outer margin of fixed finger of large chela smooth or only bearing basal spines; either antennular flagella or palm of large chela banded 11
- 11a. Spines of abdominal pleura IV and V reaching posterior margins of pleura; antennular flagella banded, palm of large chela not banded, lateral carapace with very large ocellus
..... *E. holthuisi*
- 11b. Spines of abdominal pleura IV and V not reaching posterior margins of pleura; antennular flagella not banded, palm of large chela banded, lateral carapace with a network of streaks *E. voigtmanni*

(Only *E. antillensis* and *E. callistus* are found in the Atlantic, all other species occur in the Indo-Pacific.)

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Table 2. Distinguishing characters amongst species of *Enoplometopus*.

Carapace teeth (lateral+intermediate+ median/postcervical)			Rostrum	Maxilliped III ischium distoventral spine	Large chela
Carapace teeth (lateral+intermediate+ median/postcervical)	Postcervical tooth				
<i>E. crosnieri</i>	2+1+6/1	well-developed	2 lateral teeth, overreaching antennular peduncle	present	surface sharply tuberculate; fingers outer margins spinose, dorsal hinge with 1 spine
<i>E. macrodontus</i>	2+1+5/1	well-developed	3-4 lateral teeth, overreaching antennal peduncle	present	surface smooth; fingers outer margins more or less spinose, dorsal hinge with 2 spines that becoming massive in large males
<i>E. callistus</i>	2+1+5/1	well-developed	3-5 lateral teeth, more or less to tip of antennal peduncle	present	surface smooth; fingers outer margins more or less spinose, dorsal hinge with 1 spine
<i>E. occidentalis</i>	3+2+5/1, anteriormost median tooth sometimes as elevated triangular plate	well-developed	2-4 lateral teeth, more or less to tip of antennal peduncle	absent	surface tuberculate; fingers outer margins more or less spinose, dorsal hinge with 1 spine
<i>E. pictus</i>	3+2+5/0	absent	3-4 lateral teeth, to tip of antennal peduncle	absent	surface sharply tuberculate; fingers outer margins spinose, dorsal hinge without spine
<i>E. chacei</i>	3+2+4/1	small, but tip distinctly separated from carapace	2 lateral teeth, overreaching antennal peduncle	absent	surface sharply granular; fingers outer margins more or less spinose (fixed finger) or only with distal spines (movable finger), dorsal hinge with 1 spine
<i>E. debelius</i>	3+2+4/1	small, but tip distinctly separated from carapace	usually 3 lateral teeth, failed to reach tip of antennal peduncle, 1.4-1.6 times as long as basal width	absent	surface sharply granular; fingers outer margins more or less spinose (fixed finger) or only with distal spines (movable finger), dorsal hinge with 1 small spine

Table 2. Continued.

	Carapace teeth (lateral+intermediate+ median/postcervical)	Postcervical tooth	Rostrum	Maxilliped III ischium dorsoventral spine	Large chela
<i>E. daumi</i>	3+2+4/1	small, tip almost level with carapace	usually 3 lateral teeth, not exceeding antennal peduncle, 1.7–2.0 times as long as basal width	absent	surface sharply tuberculate; fingers outer margins spinose (fixed finger) or only with distal spines (movable finger), dorsal hinge with 1 small spine
<i>E. gracilipes</i>	3+1+5/2	well-developed	2–4 lateral teeth, not exceeding antennal peduncle	present	surface smooth; fingers outer margins and dorsal hinge both lacking spine
<i>E. antillensis</i>	3+1+5/2	well-developed	3–4 lateral teeth, more or less to tip of antennal peduncle	present	surface smooth; fingers outer margins spinose (fixed finger) or without spines (movable finger), dorsal hinge without spine
<i>E. holthuisi</i>	3+1+5/2	well-developed	3 lateral teeth, more or less to tip of antennal peduncle	present	surface smooth; fingers outer margins smooth except basal part of fixed finger with spine, dorsal hinge without spine
<i>E. voigtmanni</i>	3+1+5/2	well-developed	3 lateral teeth, more or less to tip of antennal peduncle	present	surface smooth; fingers outer margins smooth except sometimes with basal spines at fixed finger, dorsal hinge with 0–1 small spine

Table 2. Continued.

Large cheliped merus dorsal margin		Abdominal pleura	Abdominal tergite VI well- developed posterior spine(s)	Telson lateral spines
entirely spinose	distal 1/2–2/3 spinose	terminated in sharp angles, posterior margins without notch	1 median	1 pair
<i>E. crosnieri</i>				
<i>E. macrodontus</i>	distal 1/2–2/3 spinose	terminated in short spines, posterior margins without notch	1 median	2 pairs
<i>E. callistus</i>	> distal 3/4 spinose	terminated in short spines, posterior margin without notch	1 median	2 pairs
<i>E. occidentalis</i>	entirely spinose	terminated in blunt angles, posterior margins without notch	at most 1 median	1 pair
<i>E. pictus</i>	entirely spinose	terminated in blunt angles, posterior margins without notch	none	1 pair
<i>E. chacei</i>	distal 3/4 spinose	terminated in sharp angles, posterior margins without notch	none	1 pair
<i>E. debelius</i>	entirely spinose	terminated in blunt angles, posterior margins without notch	none	1 pair
<i>E. daumi</i>	> distal half spinose	terminated in blunt angles, posterior margins without notch	none	1 pair
<i>E. gracilipes</i>	entire length spinose	terminated in long spines, posterior margins slightly notched	none	2 pairs
<i>E. antillensis</i>	entire length spinose	terminated in elongate spines, posterior margins deeply notched	2	2 pairs
<i>E. holthuisi</i>	entirely spinose	terminated in elongate spines, that of IV and V reaching posterior margins of pleura, posterior margins deeply notched	2	2 pairs
<i>E. voigtmanni</i>	entirely spinose	terminated in elongate spines, that of IV and V not reaching posterior margins of pleura, posterior margins deeply notched	2	2 pairs

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Note added in proof: After this paper was accepted, Rohan Pethiyagoda from the Wildlife Heritage Trust in Sri Lanka sent the authors photographs of two species of *Enoplometopus* collected from reefs in Sri Lanka. One species was *E. crosnieri*, and the other was *E. macrodontus*. It therefore appears that both species also occur in the Indian Ocean.